The ant and the lion

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establish insect segments vary and when time of completion of that stage has been modified (Refs 14,15). Against this background we evaluate the dramatic proposal by Slack *et al.*[7] that the minimal definition of an animal can be extracted from the conserved pattern of homeotic genes in what they call the zootype. The zootype is most evident at the phylotypic stage – the vertebrate pharyngula, or the insect germ-band stage. Minelli and Schram defined a series of phylotypes corresponding to other complexes of genes that are both downstream from homeobox genes and likely to control more specific aspects of metazoan body plans (see Ref. 5 for discussion). From such gene-based definitions of animals will flow gene-based definitions of phylotypic stages.

Essential features of the development of the body plan or the conservation of phylotypic stages are constrained, limited in their variability, and maintained by stabilizing selection in large measure because of the integrated nature of the epigenetic processes that produce those stages. We need to understand how developmental processes are constrained and phylotypic stages conserved despite variability in the underlying processes. Such knowledge will have enormous implications for current theories of how animals are constructed, how structures or suites of characters are conserved through evolution, and whether phylotypic stages are real or phantoms.

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References

1 Baer, K.E. von (1828) *Über Entwickelungsgeschichte der Thiere: Beobachtung und Reflexion*, Gebrüder Bornträger, Königsberg (reprinted 1967 by Culture et Civilisation, Bruxelles)
2 Ballard, W.W. (1981) **Morphogenetic movements and fate maps of vertebrates**, *Am Zool.* 21, 391–399
3 Haeckel, E. (1876) *The History of Creation*, Appleton
4 Richardson, M.K. *et al.* (1997) **There is no highly conserved embryonic stage in vertebrates: implications for current theories of evolution and development**. *Anat. Embryol.* 196, 91–106
5 Hall, B.K. *Evolutionary Developmental Biology* (2nd edn), Chapman & Hall (in press)
6 Sander, K. (1983) **The evolution of patterning mechanisms: gleanings from insect embryogenesis and spermatogenesis**, in *Development and Evolution* (Goodwin, B.C., Holder, N. and Wylie, C.C., eds), pp. 137–160, Cambridge University Press
7 Slack, J.M.W., Holland, P.W.H. and Graham, C.F. (1993) **The zootype and the phylotypic stage**. *Nature* 361, 490–492
8 Anderson, D.T. (1973) *Embryology and Phylogeny in Annelids and Arthropods*, Pergamon Press
9 Richardson, M.K. (1995) **Heterochrony and the phylotypic period**, *Devel Biol.* 172, 412–421
10 Ballard, W.W. (1976) **Problems of gastrulation: Real and verbal**, *Bioscience* 26, 36–39
11 Carter, C.A. and Wourms, J.P. (1992) **Naturally occurring diblastodermic eggs in the annual fish *Cynolebias*: implications for developmental regulation and determination**, *J. Morphol.* 215, 301–312
12 Rieppel, O.C. (1992) **Homology and logical fallacy**, *J. Evol. Biol.* 5, 701–715
13 Medawar, P.B. (1954) **The significance of inductive relationships in the development of vertebrates**, *J. Embryol. Exp. Morphol.* 2, 172–174
14 Brusca, R.C. and Brusca, G.J. (1990) *Invertebrates*, Sinauer Associates
15 Gilbert, S.F. and Raunio, A.M. (1997) *Embryology: Constructing the Organism*, Sinauer Associates

The ant and the lion: common principles and idiosyncratic differences in social evolution

What do a pride of lions and an ant colony have in common? Did similar selective forces drive the evolution of their diverse social systems, or were taxon-specific differences all important? To tackle these questions, a workshop entitled 'Social Evolution in Vertebrates and Invertebrates: Common Principles and Idiosyncratic Differences' was held at Losehill Hall in Derbyshire, UK, in June. The organizers, Francis Ratnieks, Ben Hatchwell and Tim Birkhead (University of Sheffield, UK), and Koos Boomsma (University of Aarhus, Denmark) brought together two groups of researchers – those studying social invertebrates and those studying social vertebrates – who do not often interact. The meeting was a thundering success in enlightening us to the variety of specialized adaptations to sociality across taxa, in promoting further communication between scientists studying vertebrates and invertebrates, and in identifying important areas for future research.

At first, delegates from both camps were challenged by the task of learning to speak the same language. This was illustrated in the first set of talks on origins of societies, in which speakers studying insects concentrated on the number of independent origins of eusociality, while those studying vertebrates typically described how and why group-living originated, with special emphasis on the role of ecological constraints on independent breeding [although, in his introduction to sociality in birds, Hatchwell pointed out that adult helping behaviour in cooperatively breeding long-tailed tits (*Aegithalos caudatus*) occurs in the absence of constraints on independent breeding]. Such differences in interpretation extended beyond just semantics, and reflected fascinating differences in our approaches to the study of societies.

The recent development of skew theory[1–4] was clearly a catalyst for the meeting. Skew models combine genetic and ecological elements to predict the apportionment of reproduction among members of social groups. Steve Emlen (Cornell University, Ithaca, NY, USA) and Laurent Keller (University of Lausanne, Switzerland) defended the view that skew theory is a powerful unifying principle, providing a quantitative means of comparing societies with differing degrees of sociality. Andrew Bourke (Institute of Zoology, London, UK) also recognized the importance of skew models in explaining the stability of complex societies. However, Tim Clutton-Brock (University of Cambridge, UK) made the point that the assumptions of skew theory may not be universal. For example, current optimal skew models assume that dominants have complete control over subordinate reproduction, and that the subordinate provides significant help to the dominant[3]. Both assumptions may not be satisfied in many vertebrate societies, for example, in dunnocks (*Prunella modularis*)[5]. Walt Koenig (Hastings Reservation, University of California, Carmel Valley, USA) contended that mating skew in many social vertebrate systems can be adequately explained by incest avoidance. It was generally agreed that skew theory should not be abandoned (at least not in the absence of a superior alternative), but that skew models should be modified to accommodate particular features of given

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social systems, such as the unbalance of power that may exist between dominants and subordinates, and colonies (social groups) having more than two breeders of the same sex.

Proximate mechanisms leading to the partitioning of reproduction in animal societies are typically poorly understood, with a few exceptions. The ponerine ants are a group of ants in which workers can mate, and many species have secondarily lost the queen caste. In his excellent talk on reproductive conflicts in ponerine ant societies, Christian Peeters (Université Pierre-et-Marie Curie, Paris, France) described how the ability of an individual worker of *Diacamma* sp to mate can be irreversibly turned off, soon after emergence of the young female adult, by the removal of the gemmae – two small innervated appendages (homologous with wings) on the thorax. This constitutes an efficient mechanism by which the dominant individual limits the breeding opportunities of the subordinates. By contrast, in the naked mole rat (*Heterocephalus glaber*) studied by Chris Faulkes (Institute of Zoology, London, UK), the queen suppresses reproduction of subordinates by behavioural aggression. This is mediated by hormonal changes in the subordinate, and is reversible. These case studies are prime examples of how within-colony conflicts over who should reproduce are resolved.

Further reproductive manipulation occurs when individuals bias offspring sex ratio in their favour. Jan Komdeur (University of Melbourne, Australia) explained how new molecular techniques can be used to determine the sex of young chicks. His work on the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*) has revealed that, depending on the profitability of raising dispersing sons or helping daughters, females adaptively modify the sex of their single-egg clutch. Moreover, this fine-tuned adjustment is conditional, depending on both the quality of the territory and the presence of helpers.

Sophisticated mechanisms of adaptive sex ratio manipulation also occur in ants. Koos Boomsma showed that ant workers can increase their inclusive fitness by biasing the colony sex ratio in their favour. Interestingly, theory[6–8] predicts that the bias should depend on whether the mother queen mated singly or multiply, and this prediction has been upheld by empirical studies of *Formica* ants by Lotta Sundström[9,10] (Helsinki University, Finland). Boomsma also showed that sex-ratio biasing by workers generates a potential conflict between queens and their mates, because the latter gain no fitness benefit if a colony produces only males. These empirical and theoretical advances have emphasized the importance of conflicts in animal societies.

Whereas most of us represented from one to a few species of animals, Rick Grosberg (University of California, Davis, USA) single-handedly represented four phyla of clonal marine invertebrates. Grosberg's recent work is on clonal anemones that live on rocky shores. These jelly-like blobs are capable of recognizing kin, and of fighting and killing non-kin. Others, such as the hydroid *Hydractinia symbiolongicarpus*, are capable of recognizing and somatically fusing with close kin[11]. His genetic demonstration of the clonal nature of these creatures prompted him to question whether they really fit into our definition of societies, and to conclude that they do not – *if* conflict is a defining feature of a society.

Through discussion, insights into the biases that occur when we study a single system became worryingly apparent. We also discovered that the task of defining common features of societies is a very demanding one. Should 'societies' be restricted to systems where there is group defence of a common resource, more than one individual of the same sex, brood care and overlap of generations, temporal or permanent reproductive inequalities due to social interactions, and kinship?

Some social systems, such as those of the termites, ably represented by Yves Roisin (Université Libre de Bruxelles, Belgium), or the stenogastrine wasps of Jeremy Field (University College London, UK), unquestionably fit these criteria for a society. However, very few of the systems we considered fit all of them. At one extreme we find Grosberg's marine invertebrates. At the other extreme, Jan van Hooff (University of Utrecht, Netherlands) described very complex primate societies based on hierarchies, kin structure and complex behavioural interactions. To one side we have the microtine rodent populations described by Xavier Lambin (University of Aberdeen, UK), which do not generally show group-living, but – through kinship and neighbour interactions – can exhibit extraordinary population dynamics. Can these vastly different systems be considered together? There was general reluctance to agree on a definition of society based on common principles, but acceptance of the idea that societies can be considered at many different levels so long as the system under study is clearly defined.

The meeting clearly demonstrated the value of bringing together researchers with a common interest in theory, but who are specialists on different taxa. But a great deal of work is still to be done, and several fertile areas for future research were identified. The recent development of highly polymorphic molecular markers such as microsatellites will provide indispensable tools for the analysis of kin structure and partitioning of reproduction within animal societies. For example, Michel Chapuisat (Museum of Zoology, Lausanne, Switzerland) used microsatellites to reveal the internal organisation of a complex, multiple-queen ant population. Bernie Crespi (Simon Fraser University, Burnaby, BC, Canada) drew attention to the potentially tremendous wealth of social animals among non-hymenopteran insects that have yet to be studied[12]. There was also a call for further investigation into the role of incest avoidance in the evolution of societies, and more generally on the important link between mating and social systems. Further valuable avenues include studies comparing the constraints that limit the development of sociality in vertebrates and invertebrates, especially those imposed by body size, fertility and colony size.

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References

1 Emlen, S.T. (1982) **The evolution of helping. I. An ecological constraints model,** *Am. Nat.* 119, 29–53
2 Vehrencamp, S. (1983) **A model for the evolution of despotic versus egalitarian societies,** *Anim. Behav.* 31, 667–682
3 Keller, L. and Reeve, H.K. (1994) **Partitioning of reproduction in animal societies,** *Trends Ecol. Evol.* 9, 98–102
4 Reeve, H.K. and Keller, L. (1995) **Partitioning of reproduction in mother–daughter versus sibling associations: a test of optimal skew theory,** *Am. Nat.* 145, 119–132
5 Davies, N.B. (1992) *Dunnock Behaviour and Social Evolution*, Oxford University Press
6 Boomsma, J.J. and Grafen, A. (1990) **Intraspecific variation in ant sex ratios and**

the Trivers–Hare hypothesis, *Evolution* 44, 1026–1034
7 Boomsma, J.J. and Grafen, A. (1991) **Colony-level sex ratio selection in the eusocial Hymenoptera**, *J. Evol. Biol.* 3, 383–407
8 Ratnieks, F.L.W. and Boomsma, J.J. (1995) **Facultative sex allocation by workers and the evolution of polyandry by queens in social Hymenoptera**, *Am. Nat.* 145, 969–993
9 Sundström, L. (1994) **Split sex ratios in Formica ants induced by variable queen mating frequencies**, *Nature* 367, 266–268
10 Sundström, L., Chapuisat, M. and Keller, L. (1996) **Conditional manipulation of sex ratios by ant workers: a test of kin selection theory**, *Science* 274, 993–995
11 Grosberg, R.K., Levitan, D.R. and Cameron, B.B. (1996) **Evolutionary genetics of allorecognition in the colonial hydroid Hydractinia symbiolongicarpus**, *Evolution* 50, 2221–2240
12 Choe, J.C. and Crespi, B. (1997) *Social Evolution in Insects and Arachnids*, Cambridge University Press

The transformation of systematics?

There has been a restlessness in systematics for several years, but now there are decided signs of a coming of age. From a perusal of the abstracts at the First Biennial International Conference of the Systematics Association, held in Oxford, UK, in August, one might be forgiven for thinking that this development resulted from the injection of molecular methods into systematics, since decidedly over one half had at least a molecular component. But the change that arguably will have a greater impact lies in the growing trend for practitioners to demonstrate the subject's relevance to the broader community of users. Systematists, no less than specialists in other disciplines, tend to communicate more often and more comfortably with others of their kind, but several are now promoting a more outward-looking vision. While new techniques may enliven the field, this openness may be its salvation. Although just 18 of the 116 contributions at Oxford were concerned primarily with outreach by systematists to the user and sponsoring communities, this relatively small subset indicated that developments over the past decade are bearing fruit.

As in any other field, promoting systematics to a wider audience depends significantly on the presentation and communication of information. Motivation for this is largely sociopolitical (for instance, through needs arising from the Convention on Biological Diversity): facilitation is coming from information technology. It is the explosive development of IT that has done so much to help us to handle large quantities of data, whether these take the form of words, numbers, molecular sequences or images. Images are increasingly likely to dominate the products of systematics. At the Systematics Association conference, there were pleas for more illustration-based keys, handbooks and monographic revisions; a greater use of CD-ROM outputs; and, notably, use of the Internet to make pictures more widely accessible. Emphasis on illustrations is wholly in line with the recognition[1] that society is adopting – atavistically – a more image-based system of communication after what has been a relatively brief historical interlude of the dominance of the written word. Just as printing caused the initial shift from an image-centred world, so IT is driving and facilitating its return.

If ever a discipline is ripe for transformation through images, systematics must be it. This is not to say that images will displace ideas. Neither does it mean that taxonomic products will merely be pictorial: images and words are synergistic, and interpretation lies at the heart of any discipline. Encouragingly, illustrations are now becoming integral to computer-generated keys for a wide variety of taxa.

Some criticism of tardiness and an inward-looking approach among the systematics community (e.g. Ref. 2) undoubtedly has been valid. But, at times, problems have been emphasized without due appreciation of the efforts and achievements of those who have risen to the challenge. Systematists, concerned about recent threats to their discipline, have demonstrated its broader value, notably to ecology[3], evolution[4] and conservation/biodiversity[5]. Furthermore, many have responded by making taxonomic data available in a way more appropriate to users other than systematists. To gather large datasets is time-consuming, not only because of the magnitude of the task, but also because taxonomic collation is not simply an exercise in keyboarding, but rather one demanding much validation and nomenclatural research.

Despite the difficulties, there are now many taxonomic compilations that owe their existence significantly to the availability of personal computers with their increasingly flexible software, expanding storage capacity, and ever rising processing speed. At the Systematics Association conference, there were several examples of the value of assembling names and associated data into an integrated system for use in producing checklists, catalogues and monographs, whether on a global basis (Leguminosae, conifers, geometer moths), or regionally (vascular plants of Meso-America). Two messages arise from these examples. One is that, given the right resources, large taxonomic facilities can be compiled in a timely fashion. The other is that from global databases, regional products can be derived.

Regionalism has always been a serious problem in systematics. It has led to the creation of numerous synonyms and over-splitting of taxa, particularly by those systematists isolated from major taxonomic institutions and thus comparative collections. But, given the emphasis of the Convention on Biological Diversity in 1992 on the national management of biodiversity, the need for regional works is of paramount importance. The difficulty of treating species-rich genera in (regional) floras was highlighted at the conference, with one conclusion that generic delimitation cannot be resolved in such works. Part of the answer to this dilemma is to network regional research efforts to produce a global whole. Modern flexible databases provide hope at least that the global–regional tension in systematics can be eased. Real solutions will depend significantly on the determination of systematists to place any regional focus in a global context.

In fact, much has already been achieved[6], and it is high time that criticism of taxonomy is at least tempered by recognition of the advances. The very existence of around 60 large, global taxonomic databases can hardly be ignored. There is, furthermore, an impressive means of access to many of these databases thanks to the existence of interoperability software developed for Internet use (Frank Bisby, University of Southampton, UK), which forms part of the ambitious Species 2000 programme. The development and growth of the computerized Taxonomy Resource and Index to Organism Names (TRITON) (Michael Dadd and Judith Howcroft, BIOSIS, North Yorkshire, UK), is an acknowledgement of the need for a centralized archive of verified names.

The demand for high-quality interpretations of substantial quantities of data has an implication for the practice of systematics. Unlike the situation experienced by systematists concentrating on small groups of species, those involved in large revisions require access to particular resources of the kind found only in large taxonomic institutes. Broadly speaking, these resources are threefold: representative

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